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ON PRIMARILY UNADAPTIVE VARIANTS[1]

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This paper deals with vertebrate *variants* (forms or species of animals more or less related but differing from one another) which, although geographical, are not direct or obvious responses to the environment.

Several types of variants are defined. Representative forms occupying adjacent regions are designated as *adjacent* races or species: Forms intermediate in structure between adjacent forms and occupying territory remote from them as *foreign intermediates:* Related forms occupying the same territory and contrasted in superficial characters as *complements:* Forms separated geographically and showing greater resemblance (not induced by environmental adaptation) than their degree of relationship would presuppose, as *outcrops.*

The hypothesis is advanced that, probably on account of competition, closely related forms are antagonistic.[2] That is, when in touch geographically they tend to force one another apart in superficial characters. If this hypothesis, which seems to fit into certain known facts extremely well, be accepted, it involves a centrifugal force in Evolution opposed to the centripetal tendencies of blood relationship.

It is the main theme of the paper to advance the concept of these two forces as the fundamental framework of evolutionary control, the helm which is swayed by natural selection or other forces.

Larus marinus (the great black-backed gull), which breeds in the north and reaches our latitude only in winter, finds its nearest relative not in an equatorial species, but in *Larus dominicensis* of the southern hemisphere, below 10° south latitude. This bird is more or less of an intermediate between *Larus marinus* (the great black-back), and *Larus fuscus* (the lesser black-back) which occurs with the former in Europe and is represented by allied forms eastward to the Pacific coast of North America, the mantle of *dominicensis* is very dark as in the larger bird; its size about that of the lesser ones. These are four in number—*Larus fuscus* occurs in Europe east to the Dwina, *Larus affinis* from the Dwina eastward across Asia, *Larus schistisagus* in northern Japan and Bering Sea, *Larus occidentalis* on the west coast of the United States. The four birds of this series are most readily separated by size and proportions of feet. *Affinis* resembles *schistisagus* in the former, *fuscus* in the latter; *schistisagus* resembles *affinis* in the former, *occidentalis* in the latter. That is *affinis* and *schistisagus* are more or less intermediates structurally between the species they separate geographically. For convenience we will call them ''adjacent intermediates'' as opposed to *dominicensis* which we will call a ''foreign intermediate'' between *marinus* and birds of *fuscus* group.

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[1] Paper read before the Section of Biology of the New York Academy of Sciences, February 14, 1916.

[2] See Darwin, "Origin of Species," p. 57. "We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature."

A species of vertebrate animals distributed over a wide geographical area often varies in the different regions it inhabits sufficiently to be separable into different intergrading races. Ordinarily no two of these races from the very nature of their origin will be found inhabiting the same region, sometimes they mingle in migration. Often these races are in direct response to different environmental conditions, but sometimes this response can not be traced. Such races form a series comparable to the gulls of the *Larus fuscus* group, and we may call them ''adjacent races'' and the gulls of the group referred to ''adjacent representatives,'' also we may call *Larus dominicensis* a ''foreign representative'' of the black-backs as well as a "foreign intermediate" between the two divisions of that group.[3]

Many of the smaller gulls have a well-defined dark hood in the adult. These hooded species may be divided into two apparently natural groups, the first in which the hood is black, the second in which it is dark brown. In the former group Bonaparte's gull (*Larus philadelphia*) has a great deal of white in the primaries, making a lengthwise band in the wing, conspicuous in life. Bonaparte's gull is found in North America. In the brown-headed *Larus ridibundus* of Europe and Asia the white in the wing makes a similar conspicuous mark, so that no one seeing the two species in life could fail to note the great resemblance. They show distinctly what is ordinarily termed parallelism. Such more or less distantly related, geographically separated parallels, not environmental parallels, are of not infrequent occurrence. For convenience we will call them "outcrops."

Probably the closest relative of *Larus philadelphia* is *Larus saundersi* from the inland waters of China and Mongolia, visiting the coast in winter. This would be a foreign as opposed to an adjacent representative.

Using, for the sake of familiarity, some of the same material we have already considered, if we contrast white-winged *Larus philadelphia*, which is common in the vicinity of New York, with its closest relative common here, the laughing gull *Larus atricilla*, we will find that the two are as different as the limits of the natural black-hooded group of which they are both members will allow. The white primaries of *philadelphia* are contrasted with the unusually dark primaries of *atricilla*, the mantle of the former is pale, that of the latter dark, and there is considerable difference in size. Such contrasted co-existing allies are of frequent occurrence, let us call them "complements."

For my next example I will turn to an entirely different group of animals, the Spanish mackerels, fishes of the genus *Scomberomorus,* found in warm seas of the world. Along the Atlantic coast of America *S. maculatus* is abundant south to Florida, and *S. regalis* is abundant about Cuba, where *maculatus* is practically unknown. *Regalis* is a close ally, we may reasonably say a derivative of *maculatus,* from which it differs in the scaling of the fins, arrangement of the numerous brownish spots which ornament both species, and in minor characters. Occurring abundantly between the two and associated with one to the north, the other to the south, is unspotted *S. cavalla* (the kingfish of Florida), I will call such an interposed species an "intrusion." Incidentally *cavalla* is a complement of both *maculatus* and of *regalis.*

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[3] See Matthew, W. D., *Ann. New York Acad. Sci.*, 1915, Vol. XXIV, p. 180, "Principles of Dispersal."

All the above mentioned cases of variants have this in common: although more or less geographical they are not obvious and direct responses to the environment; probably environment has little to do with them. Apparently we get all the various types of variants as classified where such control is lacking or not essential. It is then pretty certain that variants occur when not induced by environment. Lacking contrary evidence this hypothesis is accepted, and cases where it apparently obtains are alone considered in this article, environmentally induced variants being too common and too generally discussed to need treatment here.

Let us go over the various types of variants, beginning with the simplest, and discuss them in relation to their probable origin. The admittedly inherent tendency to variation in any form would be sufficient, where the form is widely distributed, to break it up into adjacent races. Adjacent representative species are pretty obviously derived from adjacent races. Even temporary isolation so readily explains this slight advance and is so easily assumed, that perhaps we should look no further for explanation. So far we have trodden familiar ground scarcely worthy of mention, and the hypothesis, that namely, probably on account of competition, closely related forms are antagonistic, is conservative enough.

If this hypothesis which seems to fit into the known facts with surprising neatness, be accepted, the writer believes that it will explain a force in direct opposition to the commingling of blood along a line of geographical demarcation of adjacent races, tending to drive those races apart in structure and making possible the derivation from them of adjacent species without geographical isolation. In fact we find in the incompatibility of closely related forms a powerful centrifugal force for differentiating species and forcing them apart[4]—and it also explains complementary coexisting forms, as it would tend to make coexisting forms complementary and would not act to change or eliminate them if they already were so. In the case of the foreign intermediate we have a geographically isolated form less influenced by the centrifugal forces, therefore varying less, retaining intermediate or primitive characters. This centrifugal force should always be considered as balanced against blood-relationship, doubtless the chief cause of resemblance in species. In the outcrop we have a case where the centrifugal force is inoperative and the centripetal tendency brings about a parallelism different in fundamental nature from the more familiar environmentally induced parallels.

There seems to be an analogy between the outcrop and homologous rectigradations in Paleoevolution.

Having given this rather concentrated outline of my hypothesis and the class of facts it is designed to explain it will not be out of place to mention other widely scattered examples of the important classes of variants alluded to. I will begin with the foreign intermediate.

Trichiurus is a long band-like silvery fish with a filamentous tail found along the shores of warm seas, where also occur numerous representatives of the Scombroid or mackerel-like fishes. The two are utterly unlike, yet a clear line of relationship is found through intermediate forms (for instance *Lepidopus*) from the ocean depths.

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[4] See, however, Gulick, J. T., "Evolution, Racial and Habitual," 1905, p. 258.

Lepidopus and its confreres are a foreign intermediate family between the mackerels and *Trichiurus,* as *Larus dominicensis* is a foreign intermediate species between the two closely related types of black-backed gull in the north. Please note another analogy. The fundamental philogenic Scombroid characters of *Lepidopus* are a direct response to life at the surface of the mackerel group. Though an intermediate it is impossible (as it is difficult in *Larus dominicensis*) to believe that it occupies the primitive habitat of the group. Other fishes which have persisted in regions distant from the center of ichthyological competition, namely the marine shore line, as in the deep sea or in fresh waters, are in a sense foreign intermediates. Before leaving *Trichiurus* let us glance at its ancestry. The deep-sea *Lepidopus*-like fishes would have little chance in competition with the mackerels in surface waters. They form in a sense a rectigradation (again apologies to Paleontology) development from the mackerels of which *Trichiurus* is the terminal member; but *Trichiurus* is so unmackerel-like that it may and does inhabit the same waters with the mackerels; it is broadly speaking complementary to them.

The tree squirrels are connected with the ground inhabiting spermophiles through the chipmunks (*Eutamias, Tamias* and *Callospermophilus*). Our common eastern chipmunk (*Tamias*) is a boldly marked animal in appearance very much resembling the Rock Squirrel (*Callospermophilus*) of high altitudes of the northwest. The resemblance is more striking than the closeness of blood relationship would presuppose, and *Callospermophilus* may be characterized in this connection as an outcrop. The forms of *Eutamias* inhabiting the same regions as *Callospermophilus* and sometimes found associated with it, are very unlike that animal, and form a very good complement with it. The eastern chipmunk is a foreign intermediate in superficial characters between *Callospermophilus* and western *Eutamias.* Interlocking of foreign intermediate and outcrop in this case is interesting, it may or may not be significant. Inhabiting more or less the same region as *Callospermophilus,* as do western *Eutamias,* are other spermophiles. They are however speckled or plain colored, little marked for the spermophile group, complements of it, whereas widely separated from it, to the south and east occur spermophiles with sufficient striping to perhaps be considered foreign intermediates between these two northwestern types of spermophile. The above discussion will show how in a single group of mammals, ground squirrels, there exist the various types of variants which have been differentiated above in discussion of fishes and birds.

The most favorable region for fish development and the center of evolutionary competition for fishes is the tropical coral reef. A great many species have the habit of seeking protection among the projections and crevices which there occur in abundance, and these as a rule are very brightly colored, blue, yellow, green, red, or marked with bold bizarre patterns in endless variety. The theory has been advanced and quite generally accepted that the colors harmonized with the brightly colored corals, etc., over which they occurred, but the fact seems to be that although with occasional spots of color the tone of the reef as a whole is comparatively uniform, these bright-colored fishes are very conspicuous swimming over it, in fact give it a good deal of its brilliant appearance. Butterfly fish, wrasses, chromids, parrotfish, etc., belong to this bright, varied crowd. They are safe from all enemies among the labyrinths of the reef and in their evolution have not felt the necessity for concealment.[5] Neutral tones are closer the one to the other than the bright and bizarre, therefore from centrifugal force we should expect, as we find, the bright and bizarre.

Brilliant birds amidst a luxuriant foliage simulate the conditions and the security of reef fishes and frequently have similarly bright and striking plumage, especially in the males, though the sitting females may be dull. The bright colors of the males may readily have been acquired under control of similar forces. I do not mean to rob sexual selection of its reputed force, but indications are that it is not entirely responsible for all that might be laid to its door. The genus *Dendroica* of small active arboreal birds has developed numerous bright, varied and beautiful colors. Two species perhaps as closely allied as any others are the Blackpoll *Dendroica striata* and Bay-breasted warblers, *Dendroica castanea.* It is interesting to find them very fair complements, the one of the other, in plumage of the breeding male, though females and young are little different; whereas the male blackpoll resembles in color the black and white warbler, *Mniotilta varia,* a distantly related bird of the same family.

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[5] Reighard, J., Public. Carnegie Instit., Washington, 1908, No. 103.

Ten years ago the writer had the pleasure of making the acquaintance of the beautiful grey slender-billed fulmar (*Priocella*), on the southern ocean. Sometime afterwards when crossing the North Atlantic he met with the northern fulmar (*Fulmarus*) and was surprised to find the resemblance between the two so great, even carried to a light mark on the wing, very useful in field identifications. Though belonging to the same family the two species are really not very closely allied and are an example of the outcrop. Another case which might be so considered is that of the African true larks or pippits which simulate our meadow larks of the family Icteridæ in color. All passerine birds are so closely allied that the two are not too distantly related to be outcrops, but there are other reasons for thinking that this case is not a very good one, but rather a case of environmental parallelism. The black breast mark, for instance, is so common among ground birds that it probably has concealing value.

The isolated islet of South Trinidad in the south Atlantic is remarkable in that three closely related species of petrels (Genus *Æstrelata*) are indigenous to it. These are almost identical in size and build but differ markedly in color. *Æstrelata arminjoniana* is bicolored, dark above and white below, *Æstrelata trinitatis* is uniformly dark colored, *Æstrelata chionofara* resembles the former bird, but the white of the underparts spreads up the sides of the neck and on to the back, which is largely white, with dark shafts to the feathers. These birds are obviously very closely related and it is sometimes debated whether or not they are distinct species or merely color phases of one and the same thing.[6] The most convincing evidence, in favor of the hypothesis of distinctness perhaps being that *arminjoniana* and *trinitatis,* forms which have long been known to science, seem to breed on the islet at somewhat different times of the year. *Chionofara* has only recently been described and is so far known from the type specimen only.

The writer has been particularly interested in these birds and has studied them carefully with a view to forming a definite opinion as to their relationship. The bicolored type of plumage represented by *arminjoniana* is perhaps the most common in the cosmopolitan pelagic genus *Æstrelata* of which it is a member, but *arminjoniana* is separated from most of the genus by the greater development of dark color on the side of the neck forming a sort of dark collar. Several uniformly dark colored *Æstrelata* also occur in various parts of the world, comparable to *trinitatis.* The third and recently described form is complementary in color to *trinitatis,* being very white for the genus, and complementary in pattern to *arminjoniana,* having the side of the neck white instead of unusually dark.

If we had three recently evolved forms breeding on the same islet, complementary plumage is what would be expected, and that the three types of *Æstrelata* from there show such plumages is good evidence that they are bona fide forms, not color phases.

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[6] Murphy, R. C., *The Auk,* July, 1915, XXXII, No. 3, pp. 342–344.

What color phases are is a matter aside from the thread of the paper but the consideration of this case has led so close to the interesting unsettled problem that the writer hopes to be pardoned for calling attention to certain things about them which he has noticed and which seem to hold good pretty well. First, they are limited to about four manifestations. The timber wolf, *Canis occidentalis* we are told is gray, white, black, or red. The gray squirrel (*Sciurus carolinensis*) is gray or black. The black bear (*Ursus americanus*) black (normal), white (glacier bear) or red (cinnamon bear). The red fox (*Vulpes fulvus*) gray (cross fox), black (silver fox) or red (normal). The screech owl is gray or red.

Students of heredity have shown that the normal gray coat of a wild guinea pig is a composite of black, white and red, which has been broken down by breeding into its constituent parts so that we get black guineas, red guineas, white guineas and guineas with the colors in patches. The colors, you will notice, are the same as those of the color phases occurring in nature and it seems probable that color phases have come about by a similar breaking down and reduction of the normal colors in a species, and have definite limits beyond which they are not likely to go.

In conclusion one might go on indefinitely demonstrating the application of the rough classification of non-adaptive variants proposed in our initial paragraph, limited only by the number of forms one could call to memory. If the significance of the classification has not been exaggerated it is difficult to find another theory which fits as well with the existing phenomena as the one advanced of a centrifugal force, though it is a pure theory and its acceptance a matter of individual taste.